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A WEST AMERICAN JOURNAL OF BOTANY

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A CYTOLOGICAL STUDY OF CLEISTOGAMOUS
STIPA LEUCOTRICHA

WALTER V. BROWN

INTRODUCTION

The genus *Stipa* is of some importance as a range grass in most of the temperate-zone grasslands. One species, *S. leucotricha*, is of considerable economic importance in Texas. This species is common throughout Texas east of the Pecos River and south of the Red River. It occurs in the very southern part of Oklahoma but is absent from the extreme eastern part of Texas and most of the coastal plain. In the Austin region of central Texas it is very abundant and can be described as a weed-type of grass which rapidly occupies disturbed soil and overgrazed pastures. It often continues in the succession from beginning to the end for it is frequently a minor constituent of the dominant grassland climax. However, since little of the central Texas range is occupied by the dominant association because of nearly continuous overgrazing, it usually results that *Stipa leucotricha* is one of the common good native forage grasses in this region. It is eaten by cattle and is highly regarded by many ranchers because of its abundance, long growing season and capacity to cure well on the ground. *Stipa leucotricha* is essentially a winter-growing perennial. Because it grows vigorously from September to June and after each rain during the summer, it may offer forage throughout the year.

Hitchcock (1935) reports that, "Cleistogamous spikelets with glumes obsolete and lemma nearly awnless are borne in basal sheaths just after maturity of the panicle." Dyksterhuis (1945) made a study at Fort Worth, Texas, of these axillary, often subterranean, cleistogenes and of their rôle in nature. He found that these cleistogenes were formed whether or not the normal panicle was produced and also that they were produced by plants kept clipped to one and one-half inches. He states that the species may behave under heavy grazing as a winter annual without producing flowering culms. This is accomplished by fall seedlings of cleistogamous origin producing new cleistogenes in the spring and then succumbing to summer drought. These cleistogenes, then, give this species a great advantage over other grasses, especially in heavily grazed areas, for a crop of seed is assured every year.

The present study began with an attempt to determine the chromosome number of this species from root tip mitosis but for technical reasons the exact number was not determined. While searching for anthers with pollen mother cells in the proper stage of meiosis it became apparent that the florets of the panicle are unusual and so a detailed study was made of these florets.

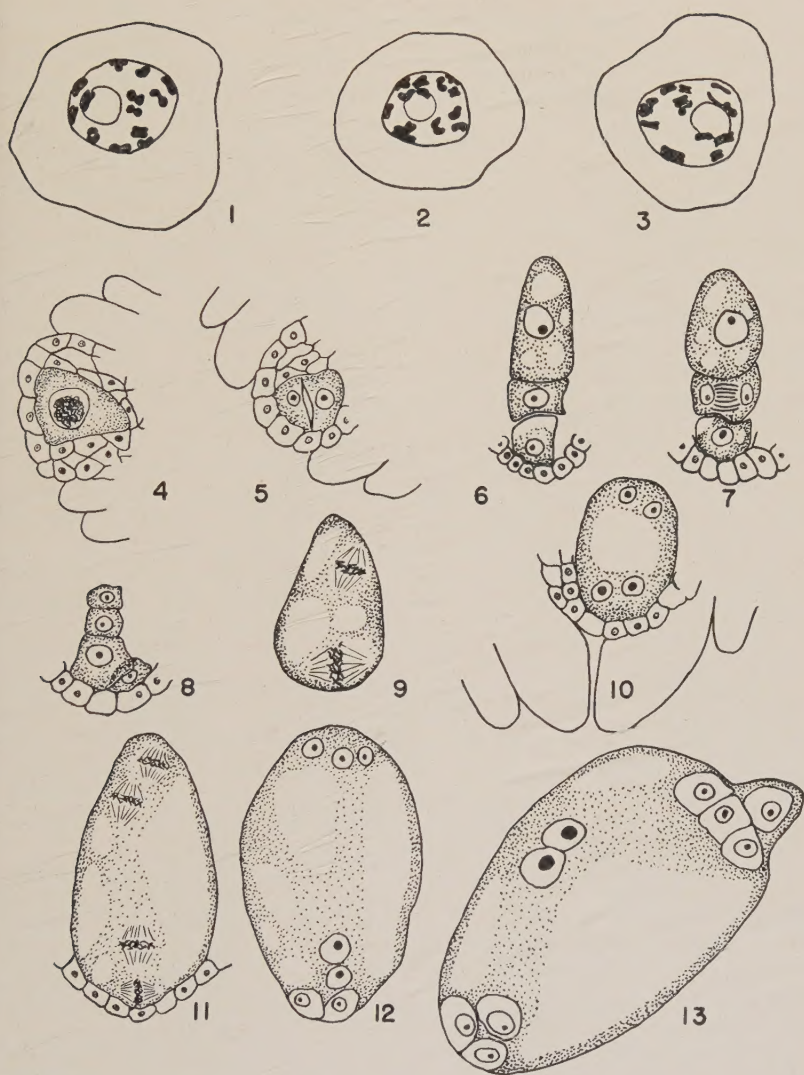
MATERIAL AND METHODS

In this work, panicle florets only were studied. Inflorescences were collected at various stages of development and florets were fixed in absolute-acetic fixative. Young florets were clipped across to permit the penetration of the fixative inside the tube formed by the lemma and palea. Older florets were dissected, and the lemma and palea were removed. Material was embedded in paraffin and sectioned longitudinally at 15 microns. Two methods of staining were employed, Heidenhain's hematoxylin, and a combination of Feulgen and fast green. The hematoxylin stain was more satisfactory.

CHROMOSOME NUMBER AND MEIOSIS

The chromosome number could not be determined from root tip mitoses by the usual method employing Craf Navashin fixative and Heidenhain's hematoxylin stain. A search for meiosis in pollen mother cells yielded no results by the smear method. Fortunately one flower was sectioned in which the pollen mother cells of one anther sac were in the diakinesis stage. There were only eight pollen mother cells in this sac and one was distorted by sectioning. The remaining seven were used in this study. Love, in Myers' text (1947) reports his material, growing under cultivation in California, to have a count of $2n = 28$. In the seven pollen mother cells studied the following results were obtained. In each of four cells 13 diakinesis bivalents were found (fig. 1), in two cells there were 11 bivalents and one quadrivalent (fig. 2) and in one cell there were 12 bivalents and two univalents (fig. 3). It is probable that this one plant had a $2n$ chromosome number of 26 which is different from Love's material. It is evident, however, that meiosis in this particular plant is quite irregular and it may be that different plants of this species have different chromosome numbers. Further study is necessary before a definite basic chromosome number can be assigned to this species.

The presence of occasional quadrivalents and univalents at meiosis in diploid species is not uncommon in the grasses. Myers (1947) lists five species that have been reported to show associations of four or more chromosomes at diakinesis. These conditions have been attributed by the authors to structural hybridity. In the present study it was not possible to determine whether the cause was structural hybridity or the presence of two pairs of homologous chromosomes. No explanation is offered for the occurrence of a pair of univalents in one pollen mother cell. Myers lists 10 species of grasses that have shown occasional univalents at first meiotic division. This list includes both diploid and polyploid species. *Stipa leucotricha* is probably diploid, for other basic numbers that have been reported in the genus are 10, 11, and 12 (Myers 1947).



FIGS. 1-13. Embryo sac development of *Stipa leucotricha*. FIGS. 1-3, Diakinesis in pollen mother cells: 1, 13 bivalent chromosomes; 2, 11 bivalents and one quadrivalent; 3, 12 bivalents and two univalents. FIG. 4, Meiotic prophase in archesporium. FIG. 5, Secondary megasporocytes. FIG. 6, Three "spore" stage. FIG. 7, Transverse division of middle "spore". FIG. 8, Enlargement of a micro-pylar megaspore. FIG. 9, Second division in the embryo sac. FIG. 10, Four-nucleate embryo sac. FIG. 11, Third division in the embryo sac. FIG. 12, Eight-nucleate embryo sac, the synergids with cell walls. FIG. 13, Mature embryo sac with four antipodal cells.

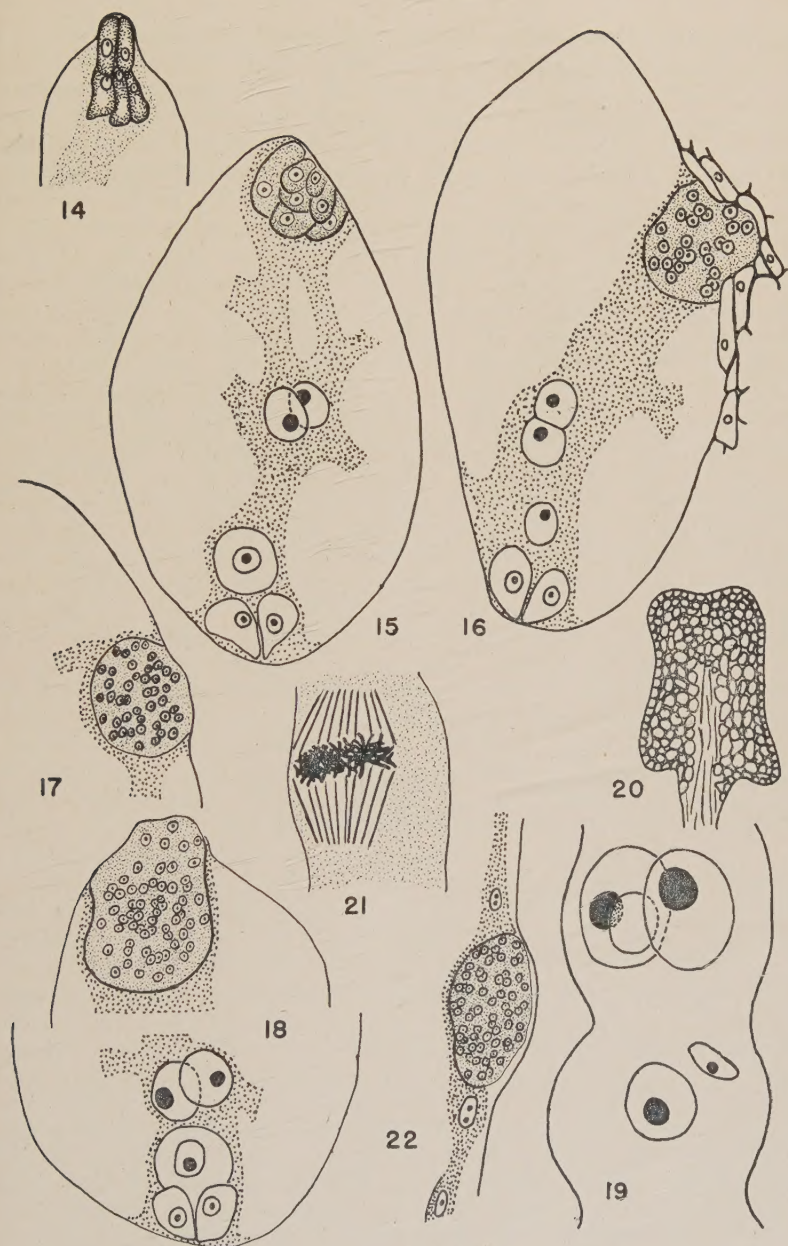
DEVELOPMENT OF THE EMBRYO SAC

The archesporial cell (fig. 4) lies immediately under the epidermal layer of the nucellus. At this stage the two integuments do not cover the terminal portion of the nucellus. The archesporial cell acts as the megaspore mother cell and meiosis takes place in it. Figure 4 shows a prophase stage of meiosis. The two cells produced are oriented so that the smaller is against the epidermis and the larger is embedded more deeply in the nucellus (fig. 5). Figure 6 shows a peculiar three-celled stage which was seen in a number of ovules. The origin of the middle cell was not determined but it arises from division of either the larger or the smaller cell of figure 5. Figure 7 shows another common occurrence, the lateral division of this middle cell. This lateral division was observed repeatedly and may well be typical of this species. Usually the spore toward the chalaza develops into the embryo sac as in figure 7 but in two cases the micropylar cell was enlarged (fig. 8). At the second division of the developing embryo sac (fig. 9) it is in contact with the epidermis and the non-functional spores are undetectable. In the four-nucleate embryo sac stage (fig. 10) the inner integument has grown around the nucellus except for the micropyle. The last embryo sac division results in eight nuclei, four at each end of the embryo sac. Figure 11 shows an orientation of the spindles which would suggest that the two synergids would be sister cells as would be also the egg and micropylar polar nucleus. This situation appears to be the rule in angiosperms for Brink and Cooper (1947) state that "... wherever definite observations have been made, the two synergids, on the one hand, and the egg cell and upper polar nucleus, on the other hand, represent sister nuclei, and no reliable observations are at hand to substantiate any other origin." Maheshwari (1948) makes a similar statement.

The mature embryo sac (fig. 12) is of the monosporic 8-nucleate, or normal type, which according to Maheshwari, "occurs in at least 70 percent of the angiosperms so far studied." All Gramineae have this normal type of embryo sac development (Schnarf, 1929). In the Gramineae, however, there is typically a further development of the antipodal cells to form a large tissue within the embryo sac. Shadowsky (1926) studied this tissue in 16 species of grasses in 7 tribes and found considerable antipodal development in all species studied. He classified them as to

EXPLANATION OF FIGURES 14-22.

FIGS. 14-22. Embryo sac development of *Stipa leucotricha*. FIG. 14, Antipodal tissue of five cells. FIG. 15, Embryo sac with antipodal tissue of seven cells. FIG. 16, Embryo sac with antipodal tissue of 24 nuclei. FIG. 17, Antipodal tissue of 42 nuclei. FIG. 18, Embryo sac at time of fertilization with antipodal tissue at end of sac with 56 nuclei. FIG. 19, Double fertilization. FIG. 20, Section of a sterile anther. FIG. 21, Division of the primary endosperm nucleus. FIG. 22, Antipodal tissue and free nuclear endosperm.

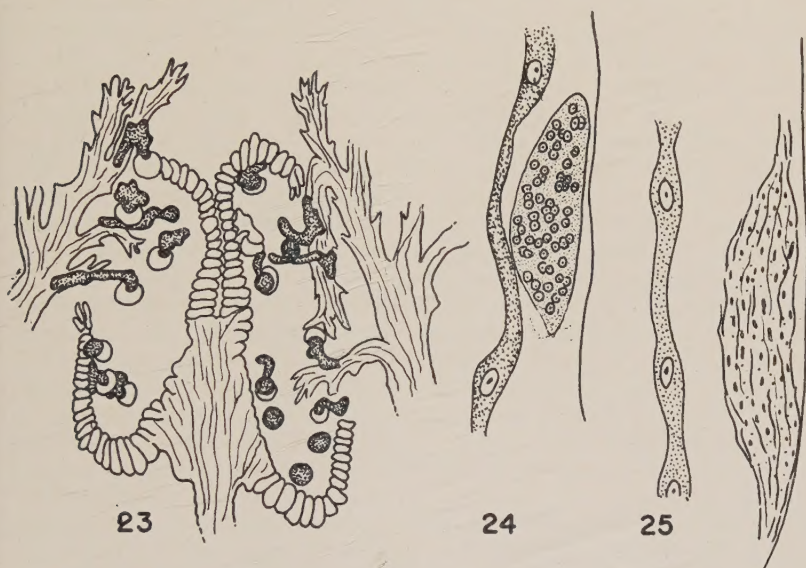


FIGS. 14-22. Embryo sac development of *Stipa leucotricha*.

whether this tissue was at the end or at the side of the embryo sac. In *Stipa leucotricha* growth of this tissue begins immediately after the 8-nucleate stage has been reached, usually by the formation first of one additional cell (fig. 13) which penetrates the chalazal tissue. It is assumed that this fourth cell is derived from one of the antipodal cells although the division was never seen nor could the chromosome number of the antipodal tissue be determined. At the same time the two polar nuclei have made contact with each other to one side of the middle of the embryo sac. These two nuclei remain in close contact in this position until just before fertilization. Figure 14 shows the 5-celled stage of the antipodal tissue, the tissue being still at the chalazal end. Figure 15 is of an embryo sac showing the 7-celled condition. The embryo sac has lengthened at the chalazal end so that the antipodal tissue is becoming lateral in position. Figure 16 shows the antipodal tissue on the lateral wall and penetrating the nucellus. There are 24 nuclei in this mass but cell walls, if they exist, could not be distinguished. The tissue is still covered by the protoplasm of the embryo sac on the inner surface. Figure 17 shows an antipodal mass with 42 nuclei. The embryo sac has increased greatly in size so that this mass is on the wall at about the middle of the sac. Rarely the antipodal mass remains terminal and moves along with the enlarging embryo sac as seen in figure 18. This mass contains 62 nuclei. The maximum number in this species seems to be about 60 nuclei since counts of 62, about 60, and 56 nuclei have been made. This compares with 30 or more in *Zea* and *Euchlaena* (Cooper, 1937), 300 in *Sasa paniculata* (Yamaura, 1933), and the various numbers reported in 16 species by Shadowsky (1926). At the time of fertilization the two unfused polar nuclei move to a position close to the egg cell (fig. 18).

Before fertilization of the egg can be effected, cleistogamous pollination (autogamy) takes place. Figure 23 represents a section of an anther and a few branches of the stigma during this process. Part of the outer wall of each anther sac disintegrates [as Uphof (1938) reports for *Cardamine chenopodifolia*] and a few stigma branches enter. The movement of these stigma branches is not caused by growth. Before the walls of the anther disintegrate these branches are confined between the palea and the anther. The disintegration of the anther walls allows the stigma branches to expand or straighten out and by so doing to enter the pollen sacs. The pollen grains germinate in place and the pollen tubes grow in various directions, some making contact with the stigma but many others never making contact. Pollen tube growth was not studied but was assumed to be normal since double fertilization took place. Figure 19 shows an egg with a male nucleus within it and shows the other male gamete in contact with the two still unfused polar nuclei. The endosperm is

triploid as a result of this triple fusion. Figure 21 represents the first division of the primary endosperm nucleus. The exact chromosome number could not be determined. Thirty-four chromosomes were counted and there were a few chromosomes remaining but uncountable. This is a few less than the expected triploid number, 39.



FIGS. 23-25. Embryo sac development of *Stipa leucotricha*. FIG. 23, Germination of pollen within anther sacs. FIG. 24, Antipodal tissue and free nuclear endosperm. FIG. 25, Disintegrated antipodal tissue and free nuclear endosperm.

The growth of the endosperm is much more rapid than that of the embryo. When the proembryo consists of four cells the endosperm consists of 28 free nuclei scattered in a thin layer of cytoplasm. Figure 22 shows the appearance of the antipodal mass at this stage. There are about 60 nuclei in this mass which is located on the lateral wall about midway of the sac. The cytoplasm of the embryo sac, endosperm at this stage, covers the inner surfaces only of the antipodal mass. At a later stage, when the proembryo consists of 8 cells and the endosperm of 73 free nuclei, the antipodal mass has assumed a lens shape and is definitely outside of the endosperm cytoplasm as shown in figure 24. The antipodal mass and the number of nuclei (56 in fig. 24) do not increase during or after fertilization. At a still later stage, when the embryo consists of 22 cells and the endosperm of 288 free nuclei, the antipodal mass is considerably flattened, the cytoplasm has largely disappeared and small scattered masses of chromatin are

all that remain of the nuclei. Thin cell walls are visible at this time so it is probable that cell walls existed in the antipodal mass at previous stages. This remnant of the antipodal tissue is definitely outside of the endosperm layer (fig. 25).

DISCUSSION

Cleistogamy. The phenomenon of cleistogamy is common in the Gramineae (Chase, 1918). Uphof (1938) in reviewing the subject, devoted two pages to the grasses. In some species, as *Leersia oryzoides*, cleistogamous spikelets are normal in structure, and are produced in normal inflorescences. Other species produce normal chasmogamous spikelets in terminal inflorescences but cleistogamous spikelets in the axils of lower leaves (Chase 1918). Usually these axillary cleistogamous spikelets (cleistogenes of Chase and cleistogames of Uphof) are much reduced spikelets, so greatly modified that they would not be classified in the same genus or tribe if their origin were not known. It is in this group that *Stipa leucotricha* has been included by Hitchcock (1935) and Dyksterhuis (1945). Observations on plants studied in the region of Austin, Texas, in the spring of 1948 show that all stages of development up to milky endosperm take place while the spikelet is included in the upper leaf sheath. Normal anthesis in grasses takes place some time after the inflorescence has emerged from the sheath and so it would be reasonable to assume that an emerging inflorescence of *Stipa leucotricha* would consist of florets in preanthesis. It is here shown that the panicle spikelets were cleistogamous in the plants studied cytologically and those observed in the field in 1948. The presence of axillary cleistogenes in many of the plants studied was confirmed. It is significant that the two years 1947 and 1948 were severe drought years in central Texas whereas the spring of 1949 had more than average rainfall.

Uphof cites many cases in which environmental factors have been shown to produce cleistogamy in plants although no case is cited in the Gramineae. It is evident that some such factors, especially available soil water, are responsible for cleistogamy in *Stipa leucotricha*, since plants of this species that produced chasmogamous florets with open pollination in the spring of 1949, had been in 1948, completely chasmogamous. Nevertheless, even in 1949, there were cleistogamous florets scattered among the chasmogamous. The grass *Bromus catharticus* behaved much the same way and in both cases inflorescences produced late in the spring under dryer, hotter conditions contained a larger proportion of cleistogamous florets or were completely cleistogamous.

Reduction of flower parts, often correlated with cleistogamy, occurs in the florets of this grass. The awn of the axillary cleistogenes is greatly reduced but the condition of other structures has

not been studied. In the panicle florets the awn is normal in development but the three anthers are small, less than 1 mm. in length. Usually two of these anthers are smaller than the third and are sterile, producing no pollen (fig. 20). In a few florets one or both of these small anthers produced a few pollen grains in one or both of the anther sacs but this was unusual. The fertile anther itself may produce as few as eight pollen grains though usually more. Such small anthers are found in cleistogamous florets of other grasses; *Bromus catharticus*, *Triodia pilosa*, *Chloris andropogonoides*, etc., whereas chasmogamous florets of the same species or related species are much larger.

Embryo sac development. The development of the embryo sac of *Stipa leucotricha* is normal and typical of grasses. Reduction division takes place in the archesporial cell. Although the full course of meiosis was not seen, one early prophase stage has been drawn in figure 4. That reduction does take place in megasporogenesis is established almost conclusively. Figure 9 shows the metaphases of the second division in the embryo sac. In one of these the chromosomes are so spaced that nearly all can be counted. Eleven chromosomes plus a few (2 to 4) were found. In figure 11 the chromosome number could be estimated as between 10 and 15. This was true also in another embryo sac observed in nearly the same stage. Finally, the first division of the primary endosperm nucleus showed 34 plus a few chromosomes (fig. 21).

Double fertilization takes place normally. Brink and Cooper find that in *Hordeum jubatum* the antipodal mass at the time of fertilization occupies about one-quarter of the space in the embryo sac and that during the course of gametic union (two hours or less) this mass increases to over six times its former volume. This is not the case in *Stipa leucotricha*. At fertilization the antipodal mass never reaches a volume one-quarter of that of the embryo sac. Furthermore the antipodal mass of *Stipa* does not increase in volume at all during or after fertilization as Brink and Cooper report in *Hordeum*. In *Stipa* this mass reaches its full development shortly before fertilization and remains of the same volume until its protoplasm disappears. Shadowsky, Brink and Cooper, Schnarf and others have postulated a glandular or food transport function for the antipodals. In *Stipa* it appears more likely that protoplasm is formed and food materials are stored in this tissue during a period when there is no growth of any other structure within the embryo sac except perhaps some cytoplasm and a great deal of vacuole. Following fertilization, however, there is a slow growth of the embryo and a rapid growth of the endosperm. Much of the food for the rapidly growing endosperm is probably derived from the embryo sac cytoplasm, from the contents of the large vacuole and, in the case of grasses, from the antipodal tissue.

It is difficult to assign to the antipodal tissue of *Stipa leucotricha* the rôle of the conducting tissue between the ovule and the embryo sac, as Schnarf has done for angiosperms in general and Shadowski and Brink and Cooper have done for a number of grasses. The antipodal tissue is located on the side of the embryo sac adjacent to the funiculus but removed from it by many parenchyma cells, as Brink and Cooper also show in their figures. However, these authors state that Schnarf attributes a significant nutritive rôle to the antipodals. They quote three statements to this effect, among them, "the position of the antipodals at the base of the embryo sac, where in general the conducting tissue of the ovule terminates, points to the assumption that the incoming material must pass through the antipodal region." This hardly applies since in many grasses, *Hordeum jubatum* and *Stipa leucotricha* included, the antipodal mass is about midway of the lateral wall of the embryo sac and not at the base of the sac. This antipodal tissue may be glandular as the latter authors indicate but it is not proved. Certainly many plants form endosperm without this tissue, in fact, with no antipodals at all. It is true, however, that in *Stipa* there is not the rapid growth of the antipodals following fertilization. This may be a basic difference between this species and *Hordeum jubatum* for it is at that time, when the antipodals increase to a volume six times their former volume, that Brink and Cooper speak of these "activated antipodals" and "aroused antipodals" with secretory activity. The antipodals of *Stipa leucotricha*, then, are not glandular, as are those of the intergeneric cross of Brink and Cooper. Another difference between *Stipa* and *Hordeum* is that in *Hordeum*, as Brink and Cooper point out, "The antipodals are a prominent and presumably active tissue in normal *H. jubatum* throughout the period when the endosperm is free nucleate. They quickly decline when the rapidly developing endosperm becomes cellular." In *Stipa leucotricha*, on the other hand, there is nothing left but cell walls while the endosperm is still free nucleate. From the present study it seems most reasonable to conclude that the antipodal tissue is storage tissue, built up when there is little growth of other tissue within the embryo sac and then used as food by the rapidly growing endosperm.

SUMMARY

The panicle spikelets in all plants of *Stipa leucotricha* that were observed at Austin, Texas, in the spring of 1948, were cleistogamous. These same plants produce axillary cleistogenes also. Of the three anthers produced in each floret, two are generally reduced and sterile while the third is reduced but produces good pollen.

Embryo sac development is of the normal, monosporic 8-nucleate type. The chalazal spore normally functions as the

embryo sac mother cell although the micropylar spore may do so occasionally. Commonly three "spores" are produced, the middle one then dividing transversely.

As is characteristic of the Gramineae, a large antipodal tissue is produced in the embryo sac. In this species the maximum number of nuclei is approximately 60. Cell walls could not be observed. The antipodal tissue reaches its maximum size before fertilization and does not increase in size thereafter. By growth of the embryo sac this tissue eventually comes to lie on the lateral wall next to the funiculus. During early stages of endosperm development this tissue lies outside of the endosperm cytoplasm. When the embryo consists of 22 cells and the endosperm of 288 free nuclei the antipodal mass has lost its protoplasm and only thin cell walls (not visible in earlier stages) remain. It appears that the antipodal tissue grows after maturity of the embryo sac when no development, other than the enlargement of the embryo sac, is taking place. After fertilization the antipodal tissue functions as stored food for the rapid growth of the endosperm.

The Plant Research Institute,
The University of Texas, and
The Clayton Foundation for Research

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A NEW SWERTIA FROM COLORADO

C. M. ROGERS

In 1947 and 1948 several collections of a species of *Swertia* were made in Las Animas and Baca counties in the southeastern corner of Colorado. Study of these specimens shows them to represent a new species.

The plant is found on gently sloping sandstone outcrops and is frequent to common over small areas in several localities. The stations for the new species lie somewhat outside of the range of the genus as delineated in recent revisions of the group (Card, 1931, St. John 1941), the nearest members, geographically, being those found along the eastern slope of the Rocky Mountains about fifty miles to the west. The present species grows at an elevation of 5000 to 5500 feet and is associated with plants which are, by and large, prairie and foothill species, such as *Arenaria Hookeri* Nutt., *Paronychia Jamesii* T. & G., *Astragalus crassicaulus* Torr., *Astragalus gracilis* Nutt., *Gilia spicata* Nutt., *Comandra pallida* A. DC., *Brauneria angustifolia* (DC.) Heller, *Chrysopsis villosa* (Pursh) Nutt., and *Palafoxia macrolepis* (Rydb.) Cory, the last named also having apparently a rather local distribution.

The affinities of the new species lie with that portion of the genus formerly included in the genus *Fraseria*, more distinctly with those species segregated as *Leucocraspedum* by Rydberg. It resembles the Californian species *Swertia puberulenta* (Davidson) Jepson in a number of characters and runs to that species in the latest key (St. John, 1941). Some differences between these two species are:

Swertia puberulenta

Inflorescence a thyrsiform cyme; peduncles clustered. Basal leaves oblanceolate to obovate, 5–10 cm. long, 1–5 cm. broad; cauline leaves narrowly elliptical, 3–5 cm. long, 1.5 cm. broad. Calyx longer or even twice as long as the corolla; calyx lobes 10–15 mm. long, corolla lobes 7 mm. long.

Swertia coloradensis

Inflorescence a corymbose cyme; peduncles opposite. Basal leaves narrowly oblanceolate, (4) 8–10 cm. long, 1 cm. broad; cauline leaves linear-oblanceolate, 4–8 cm. long, 0.6–0.9 cm. broad. Calyx and corolla of nearly equal length; calyx lobes mostly 8.5–10 mm. long, corolla lobes mostly 9 mm. long.

Swertia coloradensis sp. nov. Herba perennis, glanduloso-puberulenta; radice lignosa; caulibus pluribus, 15–20 cm. altis, cymis corymbosis; foliis oppositis, albo-marginatis, infimis lineari-oblanceolatis, (4) 8–10 cm. longis, 1 cm. latis, foliis superioribus lineari-oblanceolatis, 4–8 cm. longis, 0.6–0.9 cm. latis; bracteis

linearilanceolatis vel linearibus; pedicellis 8–12 mm. longis; floribus 4-partitis, lobis calycis linearilanceolatis 8.5–10 mm. longis, 1.25–1.5 mm. latis; corollis pallide luteolis vel albidus, intus purpureo-punctatis, lobis corollae obovatis, 7.5–9.5 mm. longis, 3–3.5 mm. latis; foveis ellipticis, 1.3 mm. latis, 1 mm. altis, margine fimbriatis, sacculis sagittatis, 0.8 mm. descendenti-bus; filamentis 5 mm. longis, antheris 2 mm. longis, 1.3 mm. latis; coronis fimbriatis, 1 mm. altis; stylis tenuibus, 3–4 mm. longis; capsulis glabris, coriaceis, modo septo parallelo compressis, ovoideis, 5–7 mm. longis, 3–3.5 mm. latis, seminibus 4, fusco-purpureis, rugulosis, 4–4.75 mm. longis.

Perennial herb with a woody taproot; stems several, 15–20 cm. high; inflorescence a corymbose cyme; leaves and floral bracts opposite, all but the uppermost distinctly white-margined; stems and leaves glandular-puberulent; stems 2.5 mm. in diam. at base, tapering upward to 0.5 mm. below the terminal flowers, first 2–4 internodes 2 mm. or less in length, those of lower and middle stem 20–30 mm. long, gradually decreasing into the inflorescence; lowermost pair of leaves sometimes bladeless, other basal leaves (4) 8–10 cm. long, 1 cm. wide, narrowly oblanceolate, obtuse or acute at the apex, narrowed to a winged petiole, cauline leaves linear oblanceolate, 4–8 cm. long, 0.6–0.9 cm. wide, floral bracts gradually reduced, the uppermost narrowly linear-lanceolate to linear, 1–1.5 cm. long, 1.5–3 mm. wide; pedicels 5–15 mm. long, pubescence similar to that of the stem; calyx of 4 slightly unequal linear-lanceolate sepals, 7.5–12.5 mm., mostly 8.5–10 mm. long, 1.25–1.5 mm. wide, narrowed to a sharp point, glabrous or with scattered hairs on the midrib below; corolla of 4 obovate petals 7.5–9.5 mm., mostly 9 mm. long, 3–3.5 mm. wide, tapering abruptly to a short mucro, pale yellowish or whitish, conspicuously purple dotted inside; foveae 2.5 mm. from the base of petals, broadly elliptic, or slightly flattened on the lower side, 1 mm. high, 1.3 mm. wide, extending downward 0.8 mm. into a flat sagittate pouch, margin fimbriate, with narrow divisions ca. 0.5 mm. long; stamens 4, alternate with petals, glabrous, filaments 5 mm. long, slender, slightly broadened near the base, anthers 2 mm. long, 1.3 mm. wide; crown 1 mm. or less high, fimbriate; style slender, 3–4 mm. long, stigmas 2, flabelliform, ca. 0.25 mm. long; fruit glabrous, coriaceous, 2-valved, flattened parallel to the septum, ovoid, 5–7 mm. long, 3–3.5 mm. wide; ovules and seeds 4, 3-angled, 4–4.75 mm. long, rugulose, brownish purple.

Type. Rocky slope, 9 miles east of Troy, near the Baca County line, Las Animas County, Colorado, June 29, 1948, *Rogers 6110* (Herb. Univ. Mich.; isotypes distributed to several herbaria).

Additional specimens examined. Six miles south of Utleyville, Baca County, Colorado, September 8, 1948, *Rogers 6423*

(description of fruit from this collection); 2.5 miles west and 2 miles north of Andrix, Las Animas County, Colorado, July 20, 1947, *Rogers 4951*; 8 miles northeast of Kim, Las Animas County, Colorado, May 31, 1948, *Rogers 5840*. (The first set of each of the above collections is deposited in the Herbarium of the University of Michigan.)

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STUDIES IN WESTERN VIOLETS, VI

MILO S. BAKER

The largest number of *Viola* species in the western part of the United States belong to the *Chamaemelum* section, most species of which have yellow or yellowish flowers. The largest group of these is the *Nuttallianae*, which contains two large species complexes, the *Viola purpurea* and the *V. Nuttallii* complexes. Each of these groups has representatives over most of the western United States, where they occupy numerous ecological niches. The more versatile of the two is the *V. purpurea* group, which occurs from near the coast of the Pacific to nearly 11,000 feet altitude in the mountains and also across the ranges and flats of the arid Great Basin.

Three species are recognized in the *V. purpurea* complex: *V. quercetorum* Baker and Clausen of the Coast Ranges and foothills of California and adjacent Oregon; *V. purpurea* Kell., with 8 subspecies occupying ecologically very different niches in the Sierra Nevada and the Great Basin; and *V. aurea* Kell., with 3 subspecies in the Great Basin. A more remote relative of the *V. purpurea* complex is *V. pedunculata* Torr. and Gray of the California Coast Ranges, with two subspecies.

The *Viola Nuttallii* complex contains the following species: *V. Nuttallii* Pursh, *V. vallicola* A. Nels., *V. Bakeri* Greene, with two, and *V. praemorsa* Dougl., with five subspecies. More remotely related are the rare endemics, *V. tomentosa* Baker and Clausen, *V. charlestonensis* Baker and Clausen, and *V. utahensis* Baker and Clausen.

The present paper treats the subspecies of *V. purpurea* and *V. pedunculata* and proposes two new combinations in *V. praemorsa*. A forthcoming paper will cover the remaining units of the *Nuttallianae*.

Cytological investigation of the group was carried on by Dr. Jens Clausen of the Division of Plant Biology of the Carnegie Institution of Washington, at Stanford. We collaborated in working out a tentative classification of the *Nuttallianae* and in testing it in the field and in the garden. Satisfactory chromosome counts have been secured for all but one of the entities in this group.

I desire to express my appreciation of the kindness of the curators who loaned us material from the United States National Herbarium (US), Gray Herbarium (GH), New York Botanical Garden (NY), Chicago Natural History Museum (F), Stanford University (DS), Pomona College (POM), University of California at Berkeley (UC), California Academy of Sciences (CAS), Missouri Botanical Garden (MO), State College of Washington (WTC), Academy of Natural Sciences of Philadelphia (PH), and Willamette University (WILLU).

Special thanks go to Dr. Jens Clausen and Dr. David D. Keck for invaluable advice and assistance in the preparation of this and the other publications on this group.

For the drawings of pistils, stamen-sheaths and seeds, I am indebted to Mrs. N. Bunyan (née Vanette Ott).

VIOLA PURPUREA Kell. Proc. Calif. Acad. Sci. 1: 55. 1855.

Plants with a strong woody taproot from the lignified rootstock but few if any adventitious roots; stems conspicuous even during the flowering season; first leaves \pm rounded \pm purple-tinted, particularly on lower surface, more succulent and differently margined than the later leaves; herbage microscopically puberulent throughout; peduncular bractlets minute, filiform, subopposite or somewhat separated; flowers bright yellow on the face, purple-tinted on back of the upper petals, varying somewhat in size between subspecies, the spur uniformly short, 1-2 mm. long, the lateral petals clavate-bearded; sepals linear-lanceolate with inconspicuous auricles, glabrate to densely puberulent, or ciliate; style length somewhat various; ovary microscopically puberulent; style with conspicuous flexure near the ovary and a capitate head with retrorse bearding on each side; stigma a minute lip terminating the head; capsule nearly spherical, microscopically puberulent; seeds more nearly spherical than in the other species of *Nuttallianae*. The caruncle does not project beyond the point of the seed but is much the same in all the subspecies except *venosa* and *atriplicifolia* in which it has a peculiarly flattened and fluted appearance when dry. The stamen sheath and its collar-opening is similar in form but varies in size for the different units of the *V. purpurea* complex. It is fully explained elsewhere (Madroño 3: 52, 53, and 57, 1935). (See also figs. 9, 12, 13, 14, pl. 8).

VIOLA PURPUREA subsp. *typica* Baker and Clausen, nom. nov.
V. purpurea Kell. Proc. Calif. Acad. Sci. 1: 55. 1855.

In strong light a depressed plant, in shade more or less erect, 6–19 cm. high; early foliage green but more strongly purple-tinted and more succulent than in the other subspecies, glabrate on upper surface; main stems 1–8, at flowering stage 4–19 cm. long, later in season longer; radical leaves 1–5, orbicular, margination irregular, 1.6–3 cm. wide, 1.8–3.5 cm. long, on petioles 4–11 cm. long (pl. 4), the stipules \pm scarious, adnate to petiole, free tip triangular to lanceolate, 2–3 mm. long; upper cauline leaves ovate, more regularly crenate-serrate, becoming microscopically puberulent throughout, the stipules foliaceous, very unequal even for the same leaf, mostly ovate to oblong, coarsely toothed, 1.5–5 mm. wide, 3–14 mm. long; peduncles 3–10 cm. long, exceeding the leaves, the bractlets filiform, mostly above the middle, never near the flowers, 2–5 mm. long; sepals glabrate to ciliate or densely short-puberulent, 1–1.3 mm. wide, 4–6 mm. long; style 2.1 mm. long; capsule 5–6 mm. in diameter; seeds dark brown (table 1).

Kellogg's species is without a type specimen, but there is a water color sketch of a portion of a fresh specimen from Placer-ville, California, drawn by Dr. Kellogg in 1855 and deposited at the California Academy of Sciences, San Francisco. The marked purple color of this plant identifies it as *V. purpurea* rather than *V. quercetorum* Baker & Clausen. Two markings shown in the drawing mentioned above, however, do not occur in any plants I have examined, namely, the purple color of the stigma and three purple stripes upon the capsule.

In the absence of a type for *Viola purpurea*, I wish to propose as a lectotype the following specimen which comes nearest to my conception of Dr. Kellogg's plant: With scattered yellow pines, along Highway 36, 2 miles west of Paynes Creek, Tehama County, California, altitude 1800 feet, *M. S. Baker 8655* (widely distributed to herbaria in the United States). This collection came from a low elevation for subsp. *typica*, being well within the elevational range of *V. quercetorum*, but a bud fixation showed that it has six pairs of chromosomes, the *V. purpurea* number.

In the field, subspecies *typica* can be distinguished from *V. quercetorum* by its greener aspect, more purple tinting throughout, somewhat smaller flowers, capsules and seeds, less vigorous growth and the somewhat narrower leaves, most noticeably in the small upper ones as illustrated in plate 4.

Viola purpurea subsp. *typica* seems almost invariably to be associated with yellow pine and occupies the Lower Transition Life Zone. It, together with subspecies *mesophyta*, *dimorpha* and *geophyta* should be known as the yellow pine violet. At the northern end of the Sacramento Valley the lower limit of the

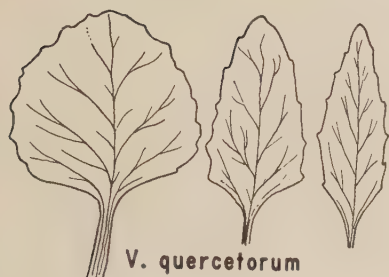
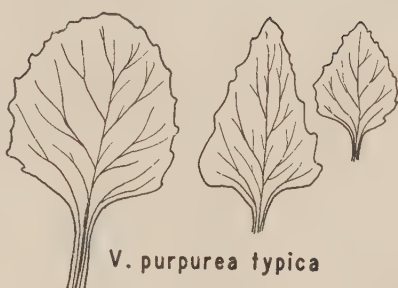
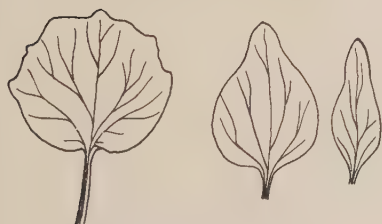
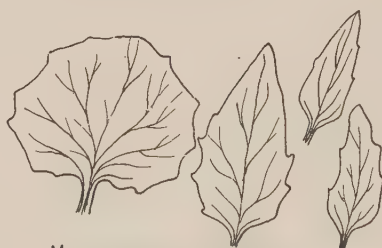
*V. quercetorum**V. purpurea typica**V. purpurea mesophyta**V. purpurea xerophyta**V. purpurea integrifolia**V. purpurea dimorpha**V. purpurea venosa**V. purpurea atriplicifolia*

PLATE 4. LEAF OUTLINES OF SUBSPECIES OF *VIOLA PURPUREA* KELL. Figures at left are earliest basal leaves, those at right, upper leaves. All $\times 1$.

yellow pine belt is around 2000 feet. From here *V. purpurea* subsp. *typica* may extend upward several thousand feet in altitude before being replaced by other subspecies.

A belt of *Viola purpurea* subsp. *typica*, generally just above a belt of *V. quercetorum*, may be found from the Mexican border, through the mountains of southern California and along the western slope of the Sierra Nevada, nearly to the western slope of Mount Lassen, thence northwesterly nearly to Mount Shasta and the Siskiyou Mountains. In the Coast Ranges it is found on Mount Pinos and the higher peaks of the San Rafael Mountains, but thus far has not been collected elsewhere to the north until Lake County is reached. Here it has been found on Mount Sanhedrin and Snow Mountain, and it doubtless grows on Mount Hull and Sheetiron. It has been collected in association with *V. quercetorum* on Elk Mountain at 4100 feet, on Mount Hanna, and at Loch Lomond, Lake County, at 2500 feet, the lowest elevation known for it in the Coast Ranges. At the south end of this lake *V. quercetorum* is abundant, while at the north end typical *V. purpurea* grows but is less abundant. This is one of the few places where the two have been observed growing side by side. No intergrading has been observed, due no doubt to their different chromosome numbers. Doubtless a considerable belt of *V. purpurea* subsp. *typica* may be found on the Yollo Bollys. In the Siskiyou, as well as in the Salmon and Trinity mountains, it has been found at the proper elevation. In the Arid Transition, north and northeast of Mount Shasta and into Oregon, subsp. *typica* is almost wholly replaced by subsp. *dimorpha*.

The altitudinal limits of subsp. *typica* are marked by the collections from Paynes Creek, Tehama County, at 1800 feet, and Cisco Grove, Placer County, at 6000 feet.

VIOLA PURPUREA subsp. *mesophyta* Baker and Clausen, subsp. nov. Planta silvicola virescens; a subsp. *typica* differt foliis erectissimis longe petiolatis, imis parvis plus minusve profunde et remote dentatis, superioribus angustis integris usque ad 5.8 cm. longis 1.7 cm. latis.

Erect green plants of coniferous forests, differing from subsp. *typica* in the strictly erect leaves, only the earliest being thick and purple-tinted and the upper being narrower, sharper, and more nearly entire, even the radical leaves (except the very earliest) are thin, elongated, with a sharper more irregular dentation and longer petioles 2.8–13 cm. long, their blades mostly ovate-lanceolate, occasionally ovate, few or none as wide as long (pl. 4), 5–22 mm. wide, 16–35 mm. long, the cauline narrower, undulate-denticulate to occasionally entire, ovate-lanceolate to oblong-lanceolate, occasionally 5 times as long as wide, 5–17 mm. wide, 2–5.8 cm. long, the petioles progressively shorter

*V. aurea typica**V. aurea mohavensis**V. aurea arizonensis**V. pedunculata typica**V. pedunculata tenuifolia**V. charlestonensis**V. tomentosa**V. utahensis*

PLATE 5. LEAF OUTLINES OF SPECIES OF *VIOLA*, SECTION *NUTTALLIANAE* OTHER THAN *V. PURPUREA*. (*Viola aurea*, illustrated here, will be treated in a forthcoming paper.) Figures at left are earliest basal leaves, those at right, upper leaves. All $\times 1$.

upwards; seeds gray, mottled with brown, dimensions and weight as in table; otherwise as in subsp. *typica*.

Type. In the shade of *Abies magnifica*, *A. concolor*, and *Pinus Murrayana*, Porcupine Flat, Yosemite National Park, Mariposa County, California, altitude 8100 feet, July 18, 1935, J. Clausen 1098 (DS; isotypes: UC, POM, MO, US).

This subspecies grows at a higher elevation than subsp. *typica*, living mainly in the upper Transition and Canadian life zones at elevations from 6000 to 10,500 feet. It is found in coniferous forests from the San Jacinto and San Bernardino mountains to the Mount Pinos region, the Tehachapi Mountains, and along the western slope of the Sierra Nevada as far north as the Feather River region of Plumas County. It is thus restricted entirely to California. Its nearest relative is subsp. *xerophyta* from which it can be distinguished by its greener aspect, longer stems, somewhat wider leaves with more rounded apices, and the forest habitat.

Near its northern limit this subspecies and subsp. *dimorpha* overlap to some extent, and might be confused because of the similarity of the uppermost leaves. A glance at one of the earliest radical leaves, however, will immediately clear up the question of identity, for that of subsp. *dimorpha* is truncate at base and the teeth are obscure or rounded, while that of subsp. *mesophyta* has a cuneate base and the teeth are more acute (pl. 4). Moreover, the uppermost leaves of subsp. *mesophyta* are considerably narrower.

At lower levels subsp. *mesophyta* may occasionally be in contact with subsp. *typica*, but the two may be distinguished both by the earliest radical leaves and the upper leaves, which are quite different (pl. 4).

VIOLA PURPUREA subsp. *xerophyta* Baker and Clausen, subsp. nov. *Nana alpina canescens cinerescens* subspeciei *mesophytæ* similis; internodiis brevibus; foliis caulinis undulato-denticulatis, superioribus anguste lineari-lanceolatis.

Alpine dwarf close to subsp. *mesophyta* but smaller, 3–12 cm. above ground, grayer because of denser puberulence, with leaves mostly narrower and stems little developed and mostly buried; taproot large, woody, without adventitious branches from the rootstock; leaves extremely variable in outline and serration but similar to those of subsp. *mesophyta* (pl. 4), the radical few; cauline leaves ovate to ovate-lanceolate or linear-lanceolate, irregularly dentate to lacerate or nearly entire, 7–15 mm. wide, 10–35 mm. long, on petioles 2–6 cm. long, the cauline progressively narrower and more acute and on shorter petioles upwards, undulate, undulate-denticulate, lacerate, or entire; peduncles equaling or much exceeding the leaves; bractlets usually near the middle of the peduncle; flowers small, about 8 mm. in diam-

TABLE 1. CHROMOSOME NUMBERS AND SEED CHARACTERS OF VIOLA, SECTION NUTTALLIANAE.

<u>Viola</u>	Chromo- some no n	Weight mg	Length mm	Width mm	Coruncle length mm	Color	Luster
<u>V. purpurea complex</u>							
V. quercetorum	12	3.29	2.69	1.79	0.64	med. brown	medium
V. purpurea							
typica	6	2.34	2.31	1.45	0.56	dark brown	dull
mesophyta	6	2.75	2.53	1.66	0.58	gray and brown	dull
xerophyta	6	2.51	2.31	1.74	0.28	mottled	dull
						gray and brown	
integrifolia	6	3.73	2.86	1.96	0.59	dark brown	dull
dimorpha	6	2.64	2.46	1.80	0.36	med. brown	dull
geophyta	6	2.00	2.37	1.52	0.40	mottled	dull
						gray and brown	
venosa	6	2.70	2.35	1.50	0.96	med. brown	dull
atriplicifolia	6	2.57	2.41	1.66	0.85	light brown	dull
V. aurea							
typica	6	2.15	2.91	1.47	0.85	med. brown	medium
mohavensis	6	2.30	2.73	1.48	0.72	light brown	medium
<u>V. Nuttallii complex:</u>							
V. praemorsa							
typica	18	6.21	3.49	2.09	1.04	light tan	shining
major	24	5.10	3.00	1.83	1.05	med. brown	shining
arida	—	4.08	2.95	1.95	0.90	light tan	medium
oregona	24	3.50	2.88	1.54	0.91	light brown	medium
linguaeifolia	18	4.24	3.25	1.81	1.34	med. brown	shining
V. Bakeri							
typica	24	4.19	3.00	1.77	0.68	med. brown	shining
grandis	24	5.16	3.56	1.98	0.62	dark brown	shining
V. Nuttallii	12	3.00	3.00	1.67	1.00	med. brown	shining
V. vallicola	6	1.70	2.19	1.27	0.78	straw color	medium
<u>Other species:</u>							
V. utahensis	12	4.40	2.97	1.65	0.77	med. brown	dull
V. tomentosa	6	2.83	2.67	1.52	0.40	light brown	dull
V. charlestonensis	6	5.04	3.42	2.08	0.50	black	shining
V. pedunculata							
typica	6	4.97	2.68	1.84	0.64	dark brown	shining
tenuifolia	6						

eter; collar-opening longer than in the other subspecies, other details of flowers as in the other subspecies; seeds gray, mottled with brown, dimensions and weight as in table 1.

Type. In open ground along the trail from Mineral King to the Little Kern River, a short distance southwest of Farewell Gap, Tulare County, California, altitude about 10,000 feet,

July 8, 1930, *M. S. Baker* 4375 (UC; isotypes: POM, DS, US).

Professor Edward Lee Greene in 1889 collected in the Tehachapi Mountains, Kern County, a violet that later was published as *Viola pinetorum* Greene. In the opinion of Dr. Clausen, this is a hybrid between subspecies *xerophyta* and *mesophyta*, and therefore the name is not available for either of these subspecies.

This subspecies is in arid alpine regions of California from the San Jacinto and San Bernardino mountains to Mount Pinos, Tehachapi Mountains and the crests of the Sierra Nevada as far north as Sierra County, extending from the Upper Canadian through the Hudsonian and into the Boreal Life Zone. One collection (*Parish 1796*) was made at 5000 feet in the San Bernardino Mountains, but usually it grows above 7000 feet, the highest known elevation being 11,000 feet on Olancho Mountain, Tulare County (*Hall and Babcock 5235*).

Attention should be called to some notable variations in this subspecies. One of these occurs in the Sierra Nevada south of Mount Whitney at Golden Trout Creek and elsewhere in this region. The leaves of this form have a markedly lacerate margin and the foliage is unusually canescent due to a dense coat of hairs approaching a tomentum. The leaves are also much narrowed, some being only one-eighth as wide as long. In the mountains of southern California and the Tehachapi there is another very narrow-leaved and highly canescent form of subsp. *xerophyta*.

The nearest relative is subsp. *mesophyta*, which is an inhabitant of forests on the western Sierra Nevada slope, while subsp. *xerophyta* occupies more open and rocky situations and extends to a higher level.

VIOLA PURPUREA subsp. *integrifolia* Baker and Clausen, subsp. nov. *Persaepe nana alpina virescens puberula*; *caulibus subterraneis*; *foliis radicalibus orbiculatis irregulariter dentatis, eis summis integerrimis*.

Alpine dwarf, mature plants showing on the surface only a clump of leaves a few centimeters high, which completely hide the buried stems; taproot woody, deep-seated, with small secondary roots and an occasional adventitious root from the rootstock; stems one to many, usually deeply buried, developed only slightly above the surface, 2-7 cm. long; herbage microscopically puberulent throughout; earliest leaves horizontal, thick and purple-tinted beneath, green above, undulate or shallowly and irregularly (never deeply) dentate, rotund with subcordate, truncate, or broadly cuneate base, 8-17 mm. wide, 10-18 mm. long, on petioles 3-5 cm. long, the cauline leaves few, smaller, narrower, mostly obtuse with cuneate base, entire, ovate to oblong-lanceolate, 3-10 mm. wide, 9-25 mm. long, on petioles progressively shorter upwards (pl. 4); stipules mostly scarious; peduncles as long as or slightly longer than the leaves, the bractlets mostly near the

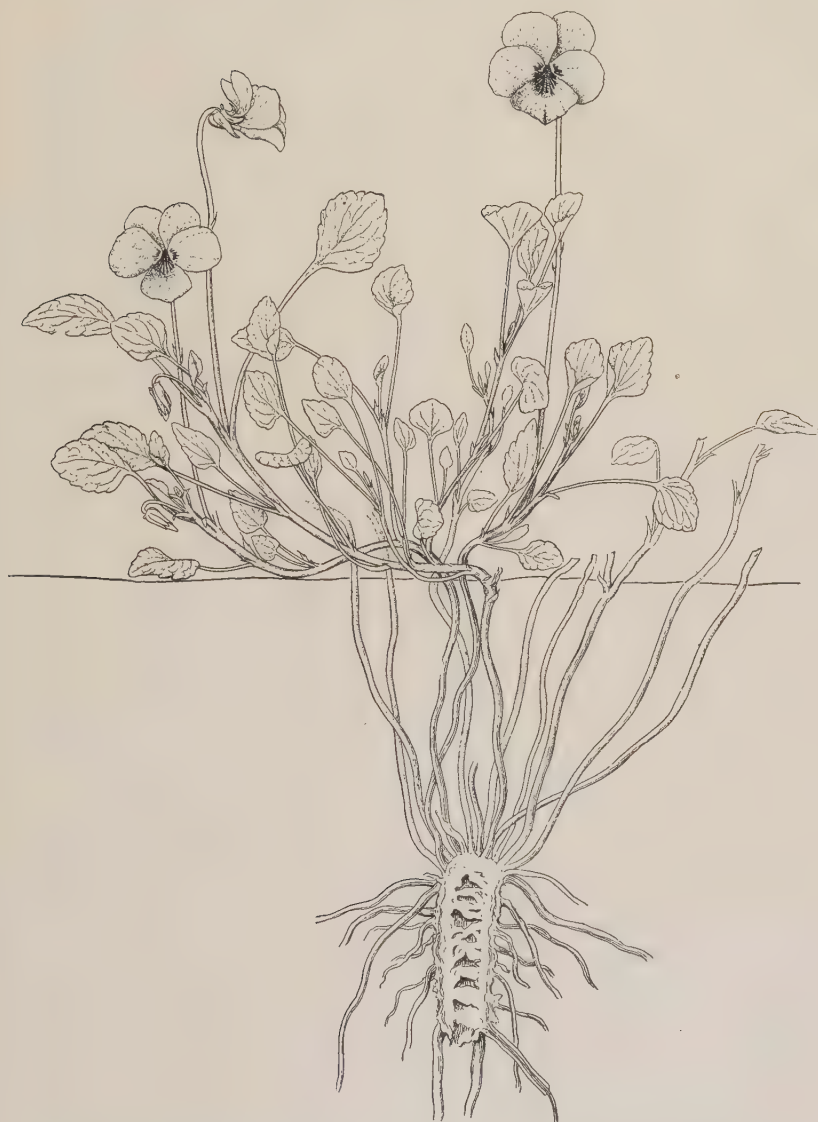


PLATE 6. *VIOLA PEDUNCULATA* TORR. AND GRAY SUBSP. *TYPICA* BAKER AND CLAUSEN. $\times 0.6$.

flowers; flowers often smaller than in subsp. *typica* but variable in size, 8–10 mm. in diameter; seeds dull dark brown, dimensions and weight as in table 1.

Type. In *Abies magnifica* forest, on the Humbug Road from Prattville to Chaparral, just north of Humbug Summit, Plumas County, California, near the Butte County line, altitude 6500 feet, June 25, 1935, *Keck & Clausen 3769* (UC; isotypes: CAS, DS, US).

In typical form this subspecies is not usually found below 6000 feet altitude and it extends upward to timber line. The highest known station is Castle Peak, Nevada County, at 8900 feet (*A. A. Heller 7089*). The subspecies is adapted to dry rocky or pumice-covered slopes as evidenced by the enormously long woody taproot. A collection from Crater Lake National Park (*Applegate 9764*) shows a taproot broken off at 20 cm. beneath the surface and a much greater length is indicated. The deeply buried buds of this subspecies enable it to withstand the extreme temperatures of high elevations.

Geographically subsp. *integrifolia* extends from Inyo and Mariposa counties north along the arid crests of the Sierra Nevada in California and the high peaks of Ormsby and Washoe counties, Nevada, to Mount Lassen, Mount Shasta, and the alpine peaks of Klamath County, Oregon. In the elevated regions about Crater Lake and south it is quite common. It also extends southward from Siskiyou County into the high peaks of the inner Coast Range where it presents a somewhat different appearance. It has been collected at 7000 feet on Snow Mountain, Anthony Peak, Mendocino County, and at the 6750 foot summit of the Covelo-Williams highway in Glenn County. In the region about this summit it is the only form of *Viola purpurea* and is abundant from 6000 to 7000 feet.

In the northern Sierra Nevada this subspecies replaces subsp. *xerophyta* at alpine levels. Though these forms overlap in the central Sierra Nevada, there is never any difficulty distinguishing them because of the greener aspect and the obtuse leaf apices of subsp. *integrifolia*.

At some points along the western borders of the Great Basin, subspecies *integrifolia* and *dimorpha* are found growing near one another. Except in northern California the entire margins of the

EXPLANATION OF THE FIGURES. PLATE 7.

PLATE 7. PISTILS OF VIOLA, SERIES NUTTALLIANAE. FIGS. 1–6, *V. Nuttallii* complex: 1, *V. vallicola* A. Nels.; 2, *V. praemorsa* Dougl. subsp. *oregona* Baker and Clausen; 3, *V. Bakeri* Greene subsp. *typica* Baker and Clausen; 4, *V. Nuttallii* Pursh; 5, *V. praemorsa* Dougl. subsp. *linguaeifolia* (Nutt. ex Torr. and Gray) Baker and Clausen; 6, *V. praemorsa* Dougl. subsp. *typica* Baker and Clausen. FIGS. 7–12, *V. purpurea* complex: 7, *V. quercetorum* Baker and Clausen; 8, *V. aurea* Kell. subsp. *typica* Baker and Clausen; 9, *V. aurea* Kell. subsp. *mohavensis* Baker and Clausen; 10, *V. purpurea* Kell. subsp. *xerophyta* Baker and Clausen; 11, *V. purpurea* Kell. subsp. *mesophyta* Baker and Clausen; 12, *V. purpurea* Kell. subsp. *typica* Baker and Clausen. All $\times 10$.

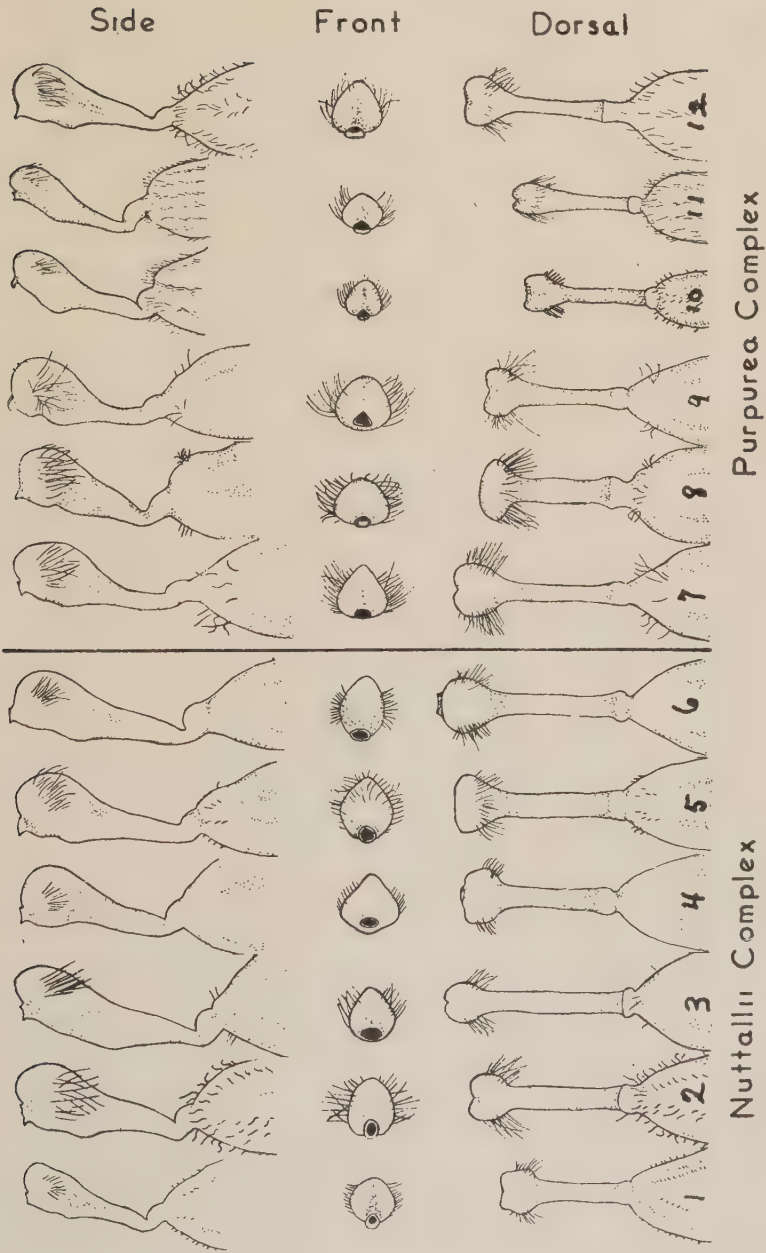


PLATE 7. PISTILS OF VIOLA, SERIES NUTTALLIANAE.

upper leaves distinguish subsp. *integrifolia*. However, in Shasta, Modoc and Siskiyou counties the upper leaves of subsp. *dimorpha* tend to have entire margins and in such a case the two subspecies are distinguished by the caulescent habit of subsp. *dimorpha*.

Discussion of this subspecies should not be concluded without comment on the peculiar form to be found about Lake Tahoe, Truckee, Hobart Mills, Webber Lake and Gold Lake. Here subsp. *integrifolia* may reach a height of 17 cm. above the soil with stems nearly as long. In the shade of the dense forests of this region the winter buds are not so deeply buried, hence the stems are mainly aerial. The aspect of these plants is wholly different from that of plants at higher elevations.

VIOLA PURPUREA subsp. *dimorpha* Baker and Clausen, subsp. nov. *Planta silvicola virescens tarde conspicue caulescens; foliis radicalibus orbiculatis basi truncatis, summis saepe integerrimis.*

Foliage greenish as in subsp. *typica*, 3–25 cm. high; early leaves rotund, truncate at base, on petioles 2–8.5 cm. long, later leaves narrowly ovate to lanceolate, obtuse to acute, truncate or slightly cuneate at base, repand-denticulate to entire, some, as season advances, 2.5–3 times as long as wide, 7–15 mm. wide, 15–30 mm. long; seeds dull brown, variable in size and form, dimensions and weight as in table.

Type. In yellow pine, white fir and incense cedar forest, near the Mineral-Chester highway, Child's Meadows, Plumas County, California, altitude about 5000 feet, June 26, 1935, *M. S. Baker* 8100 (UC; isotypes: DS, CAS, US, NY, GH, F).

This subspecies has a wide distribution in the coniferous forests bordering the Great Basin from Deschutes County, Oregon, southward through Siskiyou, Modoc, Lassen and Plumas counties, California, and along the eastern slope of the Sierra Nevada as far south as Inyo County, California.

It should be borne in mind that subsp. *dimorpha* is a forest or

EXPLANATION OF THE FIGURES. PLATE 8.

PLATE 8. *VIOLA*, SERIES *NUTTALLIANAE*. FIGS. 1–7. Pistils, side, front, and dorsal views: 1, *V. praemorsa* Dougl. subsp. *major* (Hook.) Baker and Clausen; 2, *V. Bakeri* Greene subsp. *grandis* Baker and Clausen (1 and 2 belong to the *V. Nuttallii* complex); 3, *V. tomentosa* Baker and Clausen; 4, *V. utahensis* Baker and Clausen; 5, *V. charlestonensis* Baker and Clausen; 6, *V. pedunculata* Torr. and Gray subsp. *tenuifolia* Baker and Clausen; 7, *V. pedunculata* Torr. and Gray subsp. *typica* Baker and Clausen. FIG. 8. Side view of pistil, *V. purpurea* Kell. subsp. *dimorpha* Baker and Clausen. FIG. 9. Stamen sheath, *V. tomentosa* Baker and Clausen. FIGS. 10–11. Seeds: 10, *V. quercetorum* Baker and Clausen; 11, *V. purpurea* Kell. subsp. *atriplicifolia* (Greene) Baker and Clausen. FIGS. 12–14. Stamen sheaths: 12, *V. Bakeri* Greene subsp. *typica* Baker and Clausen; 13, *V. praemorsa* Dougl. subsp. *typica* Baker and Clausen; 14, *V. pedunculata* Torr. and Gray subsp. *tenuifolia* Baker and Clausen. FIG. 15. Seed, *V. praemorsa* Dougl. subsp. *typica* Baker and Clausen. All $\times 10$.

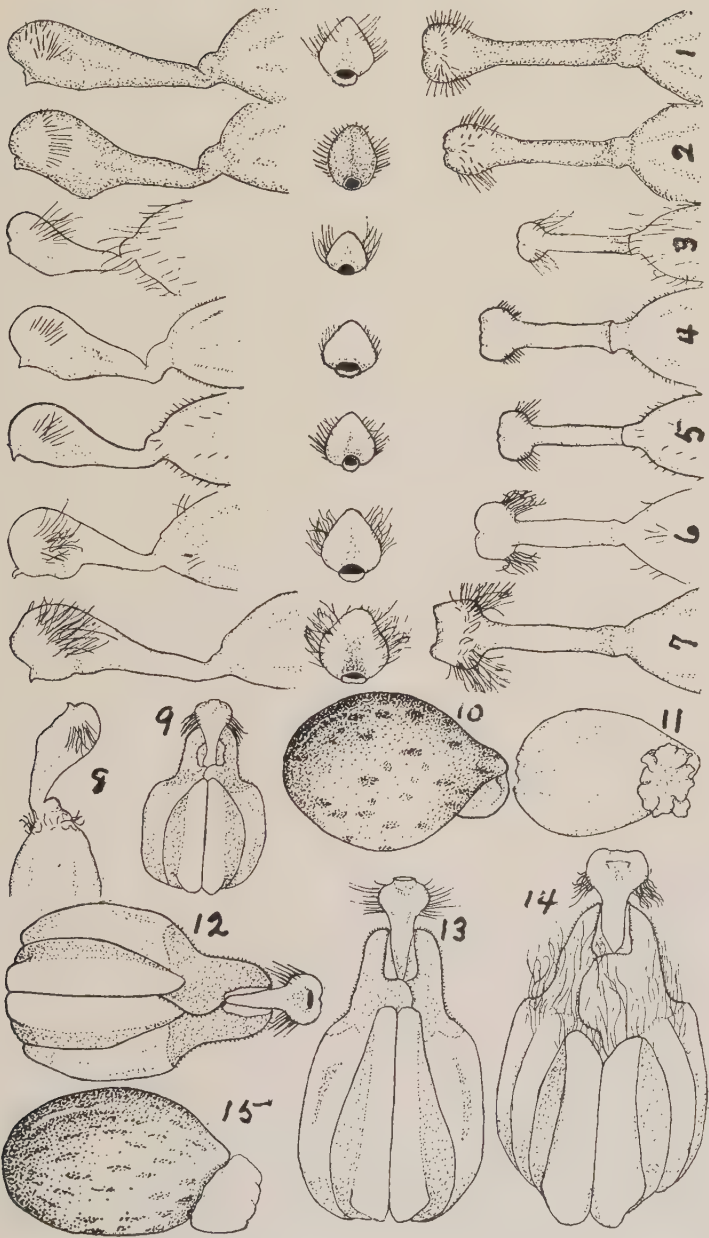


PLATE 8. VIOLA, SERIES NUTTALLIANAE.

shade type, while subsp. *geophyta* inhabits open areas surrounded by forests and is therefore a sun type. Seasonal buds of subsp. *dimorpha* are near the surface, while in subsp. *geophyta* the buds are deeply buried. These two subspecies completely intergrade at several places, however, indicating that possibly they represent but environmental forms of one unit.

Subspecies *dimorpha* shows wide variation. Early in the season the first flowers appear when the plant is extremely small and possesses few other than basal leaves. Later in the season it may be many times higher, with the rounded basal leaves all fallen and only the narrow nearly entire cauline leaves present, thus making the plant appear like an entirely different species. It is to this peculiar characteristic of the plant that the proposed subspecific name calls attention.

At the height of the flowering season subsp. *dimorpha* often closely resembles subsp. *typica* in regions where the ranges of the two overlap. However, subsp. *dimorpha* can be easily distinguished by the truncate or subcordate base of the earliest leaves, and by the narrower, more acute and more nearly entire upper leaves.

Occasionally a plant of subsp. *dimorpha* is found which may be confused with subsp. *mesophyta*, the later leaves being often very similar. In such a case, the early leaves serve to distinguish them, for the radical leaves of subsp. *dimorpha* are truncate or subcordate basally, while those of subsp. *mesophyta* are cuneate basally.

VIOLA PURPUREA subsp. *geophyta* Baker and Clausen, subsp. nov. Planta caespitosa acaulescens usque ad 5 cm. alta plus minusve cinerescens (glabrata usque ad fere canescens); foliis radicalibus orbiculatis basi truncatis, summis plus minusve dentato-serratis; hibernaculis valde subterraneis.

A low-growing geophyte with little stem development and that largely subterranean, caespitose, seldom more than 5 cm. high above ground, scarcely hairy and light green to almost canescent; root system woody, variable, but commonly with one or more adventitious branches from the rootstock; primary stems 1-6, from tip of deep-seated vertical rootstock, 2.5-8 cm. long, erect or ascending; lowest leaves (both radical and cauline) rounded, thick, purplish, coarsely, deeply and bluntly dentate, the blade commonly broader than long, 1-3.4 cm. wide, 1-2.8 cm. long, on petioles 2.5-8 cm. long, the cauline leaves progressively smaller, sharper, and grayer upwards, ovate to ovate-lanceolate, \pm sharply but not deeply dentate-serrate; stipules of radical leaves scarious, the free tip nearly obsolete, of cauline leaves mostly scarious and shrivelled but occasionally foliaceous above; peduncles of petaliferous flowers longer than the leaves, those of the more numerous cleistogamous flowers short and \pm subterranean, the bractlets scarious, nearly obsolete, near the middle; flowers and capsules

smaller than those of subsp. *typica*; seeds dull brown, finely mottled with gray, dimensions and weight as in table.

Type. In volcanic ash, yellow pine and lodge-pole pine forest, 20 miles south of Lapine on the road to Silver Lake, Deschutes National Forest, Klamath County, Oregon, altitude about 4000 feet, June 23, 1935, *Keck & Clausen 3707* (UC).

This subspecies is found in open flats of the coniferous forests along the western border of the Great Basin from Deschutes County, Oregon, southward through northern California and along the eastern slope of the Sierra Nevada as far as Mono and possibly Inyo County. Its buds are protected in winter by a layer of soil several inches in thickness. The older plants form low spreading mounds of what appear to be only leaves topped with a few flowers. Still later in the season the short stems are full of short-peduncled capsules from apetalous flowers. These cleistogamous capsules are seldom as high as the leaves when ripe and often are beneath the soil.

This subspecies is closely allied to subsp. *dimorpha* with which it sometimes intergrades as mentioned above. Both subspecies range from 4000 to 8000 feet in elevation. Three principal differences separate them: subsp. *geophyta* has more deeply buried seasonal buds, very little stem development, and a greater serration of the uppermost leaves.

Subspecies *geophyta* differs from subsp. *atriplicifolia*, which it occasionally contacts on the east and northeast, in growing at a somewhat lower elevation and in having its stems invariably buried, while subsp. *atriplicifolia* varies in this respect. The leaves of the latter subspecies are more sharply, deeply and irregularly notched, resulting in shapes reminiscent of some *Atriplex* leaves.

VIOLA PURPUREA subsp. *venosa* (Wats.) Baker et Clausen, comb. nov. *V. Nuttallii* var. *venosa* Wats. Bot. King's Expl. 35. 1871. *V. aurea* var. *venosa* Wats. in Brewer & Wats. Bot. Calif. 1: 56. 1876. *V. praeformosa* var. *venosa* Gray, Syn. Fl. 2: 200. 1895. *V. venosa* Rydb. Mem. N. Y. Bot. Gard. 1: 262. 1900. *V. purpurea* var. *venosa* Brain. Vt. Agric. Exp. Sta. Bull. 224: 111. 1921. *V. Thorii* A. Nels. Bot. Gaz. 30: 193. 1900. *V. atriplicifolia Thorii* A. Nels. Coult. & Nels. Man. Bot. Rocky Mts. 321. 1909.

Similar to subsp. *typica* except basal leaves slightly smaller, occasionally more deeply and regularly dentate, later leaves somewhat larger, more abundant, narrower and sharper at apex, the margin not so deeply broken, often entire; pubescence usually shorter, often consisting of mere points as if sanded; peduncles in fruit often recurved towards the ground; seeds dull brownish, variable in size, dimensions and weight as shown in table, the caruncle large, wide-spreading but thin, and when dry, flattened and fringed around margin, variable in size, up to 1 mm. in diameter.

The type was collected in the West Humboldt Mountains, Nevada, and the subspecies ranges from Nevada to the Wasatch Mountains, Utah, Colorado (one outlying station at Steamboat Springs, Routt County), thence northward through Wyoming to Montana, and westward through Idaho to eastern Washington. It has not as yet been found in eastern Oregon, but is to be expected there. Its elevational range is from 5000 to 10,000 feet. Except at high altitudes it grows in dense shade of forests or brush. Such shade conserves the necessary moisture to permit a longer seasonal growth, resulting in longer stems and a greater proportion of cauline leaves.

This subspecies is most baffling because of the wide variation in leaf-shape (pl. 4). The two drawings on the left represent two types of basal leaves. There is scarcely a leaf form of the *Viola purpurea* complex of the Pacific Coast that cannot be duplicated in this subspecies. Watson's type is very close to subsp. *typica* or subsp. *integrifolia*, but plants from lower elevations often have large cauline leaves which may be entire or obscurely dentate. Again, the cauline leaves may be small and greatly elongated as at the right in the plate. There is no fixed pattern in leaf outline (pl. 4) nor any other definite character except for the peculiarly flattened and fringed type of caruncle which is the same as that in subsp. *atriplicifolia* (pl. 8, fig. 11).

As shown by the synonymy, this unit has been placed by various authors under five different species, but in my opinion Brainerd was correct in classifying it as a subunit under *V. purpurea*. It has but one constant difference separating it from *V. purpurea* subsp. *typica*, and that is in the form of the caruncle of the seed. A minor difference such as this cannot justify specific separation.

The nearest relative of subsp. *venosa* is subsp. *atriplicifolia*. Both are confined to the Great Basin region and both extend to near timber line. Each has the same peculiar spreading caruncle (when dry) and a similar pubescence. They differ mainly in the leaf outline.

VIOLA PURPUREA subsp. *atriplicifolia* (Greene) Baker and Clausen, comb. nov. *V. atriplicifolia* Greene, Pittonia 3: 38. 1896.

Closely allied to subsp. *venosa* but early leaves more sharply dentate, in some cases nearly lobed, the later leaves triangular, acute, coarsely and irregularly dentate to quite entire; stem development small, never exceeding the height of the radical leaves; seasonal buds vary greatly in depth, being deeply buried at one locality and near the surface at another; in other details as in subsp. *venosa*.

Type. Dry hills near Mammoth Hot Springs, Wyoming, Yellowstone Park, altitude 6500 feet, June 1893. *F. H. Burglehaus* (US).

This subspecies has a wide distribution, mostly at fairly high elevations from 6000 to 10,000 feet (rarely as low as 5000 or even 4500 feet), from Wyoming to Idaho and southeastern Washington, southward through eastern Oregon and Nevada to Ashland Butte, the Warner Mountains of California and the eastern slopes of the Sierra Nevada as far south as Inyo County, California.

A shade form of this subspecies deserves comment for it presents a very different appearance from the plants of more open ground. The early, largely radical, leaves have greatly elongated petioles (in an extreme case 16 cm. long), and the somewhat elongated stems are feeble, bearing tiny leaves. The early leaves lack the distinct notching of the sun form; instead their irregular notches are greatly rounded, suggesting an undulate margin. Moreover, their blades are much larger, being up to 2-3 cm. in width and length, yet the cauline leaves are not larger but may be very narrow and much overtopped by the elongated basal leaves. The following collections represent this seldom collected shade form: Wallowa Mountains of northeastern Oregon, *Cusick 3074*; Ashland Butte, Jackson County, Oregon, *Applegate 5462, 5498*; western slope of the Warner Mountains, Modoc County, California, *Applegate 7960*.

VIOLA PEDUNCULATA subsp. *typica* Baker and Clausen, nom. nov. *V. pedunculata* Torr. and Gray, Fl. N. Am. 1:141. 1838.

VIOLA PEDUNCULATA subsp. *tenuifolia* Baker and Clausen, subsp. nov. A subsp. *typica* differt foliis tenuibus, superioribus vix longioribus quam latis; sepalis longioribus angustioribus acutioribusque; corollis flavis haud aurantiacis parvioribus; stylo brevior 2.1 mm. longo.

Subspecies *tenuifolia* differs from subsp. *typica* in having thinner, smaller, more acute leaves of deltoid outline, most of them being longer than wide (pl. 5). The leaves of subsp. *typica* are ovate, obtuse, and approximately as broad as long. The flowers of subsp. *tenuifolia* are often smaller than those of subsp. *typica*, sometimes not larger than those of *V. quercetorum*. At the type locality, the flowers are yellow, not orange as in subsp. *typica*. The sepals are narrower, longer, and more acute. The style is only 2.1 mm. long, while that of subsp. *typica* is 2.9 mm. Style length is one of the most dependable characters in the Nuttallianae. Also the style is conspicuously bulged downward just back of the stigmatic lip.

Type. Associated with oak and digger pine, along highway to Tres Pinos, 4 miles easterly from Pinnacles Lodge, San Benito County, California, altitude 1100 feet, April 5, 1939, *M. S. Baker 9267* (UC; isotypes: DS, POM, US, F, NY, GH).

This subspecies was found to be abundant in the Pinnacles region in rocky uplands rather than in good deep clay or bottom land soil such as that on which subsp. *typica* is found. It was

found growing in scattered colonies nearly to the top of Chalone Mountain, which is 3287 feet high.

Throughout most of its range *Viola pedunculata* exhibits very constant characters. In this area, however, subsp. *typica* does not occur but is to be found contiguous to subsp. *tenuifolia* on its south, west and north borders.

In 1902 C. A. Purpus collected *V. pedunculata* at Springville in Tulare County. Because this species had not before been reported outside the coastal area the data on the Purpus specimen were questioned. In March, 1943, Miss Ella Carter collected material from the Crawford Ranch, six miles below Trimmer Springs in Fresno County. Both of these collections are the subsp. *tenuifolia* and there seems no reason to further question the Purpus collection. These occurrences add another species to the growing list of Coast Range plants that have disjunct ranges between the Coast Ranges and the southern Sierra Nevada foothills.

In the Tertiary there was an arm of the ocean extending into the San Joaquin Valley in the region where this violet has been collected. This may explain its presence as small relict colonies in an arid region where it is possibly doomed to final extinction.

VIOLA PRAEMORSA Dougl. subsp. *linguaefolia* (Nutt. ex Torr. and Gray) comb. nov. *V. linguaefolia* Nutt. ex Torr. and Gray, Fl. N. Am. 1: 141. 1838.

VIOLA PRAEMORSA Dougl. subsp. *major* (Hook.) comb. nov. *V. Nuttallii* var. *major* Hook. Fl. Bor. Am. 1: 79. 1830.

Kenwood, California

NEWS AND NOTES

DISPOSITION OF THE WILLIS LINN JEPSON ESTATE. The estate of Willis Linn Jepson who died on November 7, 1946, was recently accepted by the Regents of the University of California for the Department of Botany on the Berkeley Campus. The will provides an endowment fund of \$320,000 and stipulates that it be used for the care and maintenance of the Jepson herbarium (estimated at 40,000 specimens) and library, the completion of the "Flora of California," the revision of the "Manual of the Flowering Plants of California," and the furtherance of studies on the flowering plants of California and adjacent areas. The research funds are to be administered for the Regents by a committee whose initial membership, as set up in the will, comprises Dr. Alva R. Davis, Professor of Botany and Dean of the College of Letters and Science as chairman, Dr. Helen Mar Wheeler, Research Associate in Botany, and Dr. Lincoln Constance, Professor of Botany. One of the foremost tasks of this committee will be to see that this invaluable material, the basis for Dr. Jepson's published works, is properly mounted and housed.

—L. CONSTANCE.